The Conservation Relevance of Epidemiological Research into Carnivore Viral Diseases in the Serengeti

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Abstract: *Recent outbreaks of rabies and canine distemper in wildlife populations of the Serengeti show that infectious disease constitutes a significant cause of mortality that can result in regional extirpation of endangered species even within large, well-protected areas. Nevertheless, effective management of an infectious disease depends critically on understanding the epidemiological dynamics of the causative pathogen. Pathogens with short infection cycles cannot persist in small populations in the absence of a more permanent reservoir of infection. Development of appropriate interventions requires detailed data on transmission pathways between reservoirs and wildlife populations of conservation concern. Relevant data can be derived from long-term population monitoring, epidemic and case-surveillance patterns, genetic analyses of rapidly evolving pathogens, serological surveys, and intervention studies. We examined studies of carnivore diseases in the Serengeti. Epidemiological research contributes to wildlife conservation policy in terms of management of endangered populations and the integration of wildlife conservation with public health interventions. Long-term, integrative, cross-species research is essential for formulation of effective policy for disease control and optimization of ecosystem health.*

Keywords: canine distemper, carnivore conservation, epidemiology research, rabies, Serengeti

La Relevancia para la Conservación de la Investigación Epidemiológica de Enfermedades Virales de Carnívoros en el Serengeti

Resumen: *Brotes recientes de rabia y moquillo en poblaciones silvestres del Serengeti muestran que las enfermedades infecciosas constituyen una causa significativa de mortandad que puede resultar en la extirpación regional de especies en peligro, aun en áreas extensas bien protegidas. Sin embargo, el manejo efectivo de una enfermedad infecciosa depende críticamente del entendimiento de la dinámica epidemiológica del patógeno. Los patógenos con ciclo infeccioso corto no pueden persistir en poblaciones pequeñas en ausencia de un reservorio de la infección más permanente. El desarrollo de intervenciones adecuadas requiere de datos detallados de las vías de transmisión entre reservorios y poblaciones de vida silvestre de preocupación para la conservación. Se pueden derivar datos importantes del monitoreo de poblaciones a largo plazo, de patrones de epidemias y de estudios de caso, del análisis genético de patógenos que evolucionan rápidamente,*

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de muestreos sexológicos y de estudios de intervención. Examinamos estudios de enfermedades de carnívoros en el Serengeti. La investigación epidemiológica contribuye a las políticas de conservación de vida silvestre en términos de la gestión de poblaciones en peligro y de la integración de la conservación con intervenciones de salud pública. La investigación a largo plazo e integradora es esencial para la formulación de políticas efectivas para el control de enfermedades y la optimización de la salud del ecosistema.

Palabras Clave: conservación de carnívoros, investigación epidemiológica, moquillo, rabia, Serengeti

Introduction

Over the past 20 years, rabies and canine distemper virus (CDV) have been the major pathogens (disease agents) affecting wild carnivore populations (Woodroffe et al. 2004). These pathogens have characteristics that typify many emerging diseases: they are RNA viruses and they can infect, and be transmitted by, a wide range of host species (Cleaveland et al. 2001). Rabies and CDV were responsible for two recent major epidemics in the Serengeti-Mara Ecosystem (SME), an area that comprises the Serengeti National Park (SNP) and Ngorongoro Conservation Area (NCA) in Tanzania and the Masai Mara National Reserve (MMNR) in Kenya (Fig. 1). These outbreaks have brought into question the view that disease was always a "natural" regulatory component of ecosystems, stimulated research projects in the Serengeti, and raised awareness of the need to integrate veterinary epidemiology into carnivore conservation and management.

Rabies outbreaks in the late 1980s and early 1990s in the SME caused population declines in African wild dogs (*Lycaon pictus*; Gascoyne et al. 1993; Kat et al. 1995) and bat-eared foxes (*Otocyon megalotis*; Maas 1993). Between 1986 and 1991, rabies was detected by laboratory diagnosis or observation of clinical signs in 5 of 15 packs of wild dogs in the ecosystem. A further two packs disappeared following undiagnosed signs, including lethargy and weakness, and the remaining eight packs disappeared unobserved (Woodroffe 1997). During this 5-year period, all packs in the ecosystem either died or disappeared (Woodroffe 1997) and, following regional extinction of this population, no breeding packs were documented in the ecosystem for the next 10 years. In 1987 and 1988, during the period of pack losses of wild dogs, rabies epidemics also affected bat-eared foxes in the central Serengeti, killing 60% of all adult females ($n = 48$) and 20% of males ($n = 19$) and cubs ($n = 234$) of a study population (Maas 1993).

Canine distemper virus caused a dramatic epidemic in the Serengeti in 1994, affecting lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), bat-eared foxes, and domestic dogs (*Canis familiaris*) (Roelke-Parker et al. 1996). Although canine distemper (CD) had been confirmed previously in captive large cats (Blythe et al. 1983; Appel et al. 1994), the Serengeti outbreak was the first documented occurrence in free-living felids. Thirty percent of lions died or disappeared in the SNP and MMNR study areas (Roelke-Parker et al. 1996; Kock et al. 1998), leading to an estimate of 1000 fatalities across the entire ecosystem.

The Serengeti disease outbreaks played a major role in raising awareness about the potential for disease to act as a local extinction threat (in the case of rabies in wild dogs) and as a major mortality factor in high-profile populations (in the case of CDV in lions). Because rabies and CDV both have short infection cycles and cause high mortality, they cannot be maintained in small (endangered) populations because infection will eventually fade out due to a lack of new susceptible hosts. In small populations disease outbreaks are invariably triggered by contact with more abundant host populations, which act as disease reservoirs (i.e., the population, or system of connected populations, that permanently maintains infection and transmits infection to the population of concern; Haydon et al. 2002*a*). To manage disease threats effectively it is important to understand how pathogens are transmitted and maintained in these reservoir populations. In the wake of the rabies and CD epidemics, understanding the role of domestic dogs became an urgent and central objective of recent research into carnivore diseases in the Serengeti. Not only are rabies and CDV common pathogens of domestic dogs in Africa, but genetic and antigenic variants of viruses isolated from wildlife in the Serengeti are closely related to isolates from domestic dogs indicative of transmission between domestic dogs and wildlife (Cleaveland & Dye 1995; Kat et al. 1995; Roelke-Parker et al. 1996; Carpenter et al. 1998).

Determining the role of wildlife and domestic animal hosts in a reservoir system has direct practical relevance for conservation management. For example, control (or elimination) of a disease that is threatening wildlife and is maintained in a domestic animal reservoir may be feasible through reservoir vaccination, treatment, population control, or separation from the domestic animal population. Nevertheless, the approach is more challenging if wildlife reservoirs exist because therapeutic tools for wildlife are limited and control measures become much more difficult.

Five key questions have been addressed in the epidemiological studies established in the Serengeti over the past 15 years: (1) How are rabies and CDV introduced into Serengeti wild carnivore populations and what are the

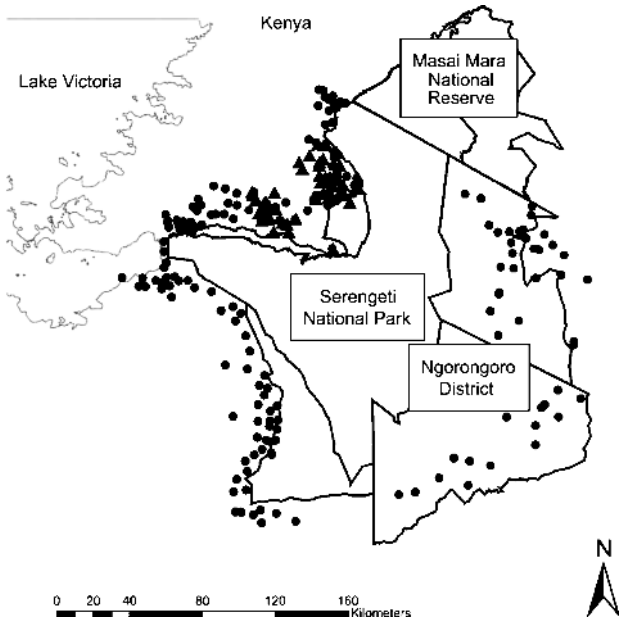

Figure 1. The location of all vaccinated villages in high-density communities to the west of Serengeti National Park and low-density pastoralist communities in Ngorongoro District to the east of the park. Mass dog vaccination trials were first conducted in villages in Serengeti District (triangles) and subsequently extended to a 10-km zone in the western districts and all villages in Ngorongoro District (circles).

key routes of transmission? (2) What threat do rabies and CD pose for wild carnivore populations in the Serengeti ecosystem? (3) What are the most appropriate immediate control strategies for these diseases, if any? (4) Where is the reservoir of infection and are these pathogens self-sustaining in Serengeti wildlife? (5) Can cost-effective control measures be integrated into a sustainable long-term strategy for park management?

Several different approaches have been used to address these questions, incorporating data from population monitoring, epidemic and case-surveillance patterns, phylogenetic analyses of pathogens, serological surveys, disease modeling, and intervention studies to explore the dynamics of viral infections and to identify reservoir systems. We examined the relevance of these findings to conservation and how they have affected both policy and practice at national and international levels.

Rabies as a Threat to Endangered Species

Although rabies is a growing public health problem throughout sub-Saharan Africa (Cleaveland 1998), the conservation relevance of the disease became apparent only following rabies outbreaks in African wild dogs in the Serengeti. Awareness of the importance of rabies in carnivore conservation has subsequently been reinforced by outbreaks in African wild dog populations in southern Africa and rabies epidemics in Ethiopian wolves (*Canis simensis*) and Blanford's fox (*Vulpes cana*; Macdonald 1993; Woodroffe et al. 2004).

In the wake of rabies epidemics in the SME during the late 1980s, concerns for the survival of wild dogs in the ecosystem were particularly acute because outbreaks were invariably associated with losses of entire packs, even though the disease may not have affected all individuals (Woodroffe 1997). This has been interpreted as a manifestation of the Allee effect (Courchamp et al. 2000) because wild dogs are obligate cooperators, and individuals may not be able to survive or breed if the pack size falls below a minimum threshold (as might occur during a disease outbreak). As a result of multiple pack losses and confirmation of rabies in SNP and MMNR packs, vaccination of wild dogs was considered by park authorities as a crisis-management tool to protect the two remaining packs in the SNP.

Reactive Disease Management—Vaccination of Serengeti Wild Dogs

Following preliminary trials in captive wild dogs, a vaccination program was initiated in the Serengeti in 1990, with inactivated rabies vaccine administered through dart inoculation to all individuals ($n = 34$) in the two known packs (Gascoyne et al. 1993). All wild dogs in these packs died or disappeared between 4 and 10 months after vaccination (during 1991). A third pack (Moru Track pack) that was not vaccinated also disappeared following a last sighting in late 1991 (Woodroffe 1997).

Following the local extinction of the Serengeti population, the association between disease outbreaks, handling of wild dogs (for radio collaring and rabies vaccination), and their ultimate disappearance was widely debated (reviewed by Woodroffe 1997; Woodroffe 2001). Several hypotheses were proposed, briefly: (1) outbreaks of rabies in wild dogs reflected the reemergence of rabies in neighboring domestic dog populations (which was absent between 1958 and 1977), with the final extinction caused by CD transmitted from domestic dogs during an outbreak in 1991 (Alexander & Appel 1994; Cleaveland et al. 2000); (2) the final demise of the wild dogs was due to rabies, which occurred despite vaccination because of the failure of a single dose to protect wild dogs from rabies (Woodroffe 1997; Woodroffe 2001); and (3) the stress of handling/vaccinating wild dogs reactivated a latent form of rabies that caused disease and death several months later (the "stress-handling" hypothesis; Burrows et al. 1994; Burrows et al. 1995).

The long-running debate surrounding the fate of the Serengeti wild dogs was generated for several reasons. First, temporal associations between events were used to provide support for each of the three different hypotheses, but there were insufficient data to demonstrate a causal relationship. Second, no samples were obtained from the packs that disappeared in the final extinction event in 1991 and therefore no diagnosis was possible to support or refute any of the hypotheses. Despite the lack of conclusive evidence, the overwhelming consensus is that the rarity of latent rabies, the long (>4 month) interval between vaccination and the disappearance of wild dogs, and the failure to detect adverse effects of handling in other wild dog populations indicate that it is highly improbable that vaccination—or any other form of handling—caused the extinction of the Serengeti wild dog population (Macdonald et al. 1992; Creel et al. 1997; Woodroffe 2001).

Despite this, the controversy of the Serengeti wild dogs has had widespread consequences for conservation and research in Tanzania and worldwide. As a result of the concerns raised by Burrows et al. (1994, 1995) about a potential link between handling and disease, research and park authorities greatly restricted levels of wildlife handling in the SME and important information could not be collected. For example, without permission to take blood samples from lions in the Ngorongoro Crater, no infection data are available for a critical period (1991–2001) when disease was identified as the most likely cause of a substantial population decline (Kissui & Packer 2004). The handling-vaccination debate has also had consequences further afield, with reluctance to grant permission to research, handle, or collar Ethiopian wolves in the late 1990s arising from concerns generated by events in the Serengeti. Rabies had been identified previously as a major extinction risk to the Bale Mountains' population of the Ethiopian wolves (Mace & Sillero-Zubiri 1997; Laurenson et al. 1998; Haydon et al. 2002*b*), and although vaccination of domestic dogs was introduced as a means of reducing the disease risk, rabies reappeared in the wolf population in 2003, resulting in a second major rabies epidemic (Randall et al. 2004). It was only in the wake of this outbreak that direct vaccination of wolves was permitted to control the spread of infection (Randall et al. 2004; Haydon et al. 2006).

On the positive side the debate stimulated analyses of the effects of handling in populations of other endangered carnivores, including wild dogs in southern Africa (de Villiers et al. 1995) and cheetahs (*Acinonyx jubatus*) in the Serengeti (Laurenson & Caro 1994), with a demonstrable lack of adverse effects resulting from the fitting of radio collars. Similarly, in the Serengeti lion population, radio-collared females lived longer than age-matched uncollared females in the same pride, and there was no difference in survival between collared and uncollared males (C.P., unpublished data). Subsequently, researchers have been careful to monitor the impact of radio collaring (Creel et al. 1997) and vaccination directly (Hofmeyr et al. 2000).

Results of a recent study demonstrate a protective benefit of rabies vaccination in South African wild dog populations (Hofmeyr et al. 2004). As a result of the debate, further work has been conducted to evaluate different vaccination schedules and delivery strategies for wild dogs (Knobel et al. 2002) and other endangered carnivores (e.g., island fox; reviewed by Woodroffe et al. 2004). The most important outcome has been the recognition of the need to design interventions as scientific trials, with inclusion of appropriate controls and allocation of resources to monitor the population and to establish cause of any deaths after intervention. These factors were clearly not considered sufficiently in the Serengeti wild dog study and can be difficult to achieve, particularly in crisis situations involving small populations. But the experience of recent trials in the Bale Mountains' population of Ethiopian wolves, which was vaccinated in the face of a rabies epidemic, demonstrates that a relatively robust study design is possible, even with critically endangered populations (Randall et al. 2004). Modeling of this epidemic further indicates that reactive vaccination is likely to have beneficial impacts by limiting the scale of the outbreak and reducing the probability of a catastrophic population decline that could result in extinction (Haydon et al. 2006).

Epidemiological Studies of Rabies in Domestic Dogs

From 1992 to 1994 preliminary epidemiological studies in and around the SNP identified two distinct populations of domestic dogs: low-density pastoralist (Maasai) dogs living in communities to the east and south of the national park, and higher-density dogs in agropastoralist communities to the west (Fig. 1). These populations showed distinctive demographic and epidemiological features. In high-density populations rabies was persistent, life expectancies were very low, and turnover rates high, whereas in lower-density populations rabies occurred only as brief and sporadic epidemics and life expectancies were much higher (Cleaveland & Dye 1995; Cleaveland 1996). This suggests that rabies can be maintained only in higher-density populations to the west of the park and these populations, as the putative reservoir, became the focus of subsequent vaccination trials.

A further finding was the detection of rabies antibody (rabies seropositivity) in a proportion (5–10%) of unvaccinated domestic dogs, none of which developed clinical signs of rabies (Cleaveland et al. 1999). Although rabies antibody is classically thought to be detectable only as or just before clinical signs of rabies appear, these results are consistent with nonfatal exposure. Seropositivity was also detected in Serengeti wild dogs prior to the vaccination

campaign (Gascoyne et al. 1993), which Burrows et al. (1994, 1995) interpreted as evidence of latency in support of the stress-handling hypothesis (i.e., that animals were harboring virus that was reactivated). Nevertheless, in both domestic dogs and African wild dogs, we consider seropositivity as more likely to have arisen from "aborted infection," with the immune response resulting in clearance of virus (Cleaveland et al. 1999). In contrast to the extensive debate about stress-related reactivation of latent rabies, the more parsimonious interpretation of aborted infection received relatively little attention or had little impact, perhaps because the data were published only after the main debate had taken place or perhaps because aspects of rabies pathogenesis and immunology are difficult to explain or appreciate.

CDV: Identifying the Source of Infection for Wildlife

After CDV was identified as the cause of an infectious disease epidemic causing mortality in multiple wild carnivore species in the Serengeti in 1994, the initial goals of epidemiological research were to identify the source of CDV and to assess the severity of the threat to wildlife populations. As with rabies, the CDV outbreak involved a single genetic variant of virus transmissible among lions, hyaenas, bat-eared foxes, and domestic dogs (Roelke-Parker et al. 1996; Haas et al. 1996; Carpenter et al. 1998), but the origin of the epidemic was unknown. To investigate the role of different domestic dog and wildlife populations as the source of CDV, evidence was compiled from the temporospatial pattern of clinical cases, population data from lions and domestic dogs, and serological data from lions, domestic dogs, and hyaenas.

Temporospatial Patterns of Disease

Diagnosis and detection of pathogens can be extremely difficult in wildlife populations, and intensive population monitoring is essential to determine spatial and temporal patterns of disease spread. It is no coincidence that virtually all the information about CDV in SME wildlife relates to lions and hyaenas, populations that have been the subject of intensive long-term research. From the Serengeti lion study population of about 250 animals, data were collected on 18 carcasses and 98 disappearances over a 6-month period of the epidemic. In contrast, in the remaining areas of the SME, where intensive population monitoring was not being carried out, only five carcasses were retrieved from a population of more than 2000 lions.

Although the number of confirmed CDV cases was relatively limited, the spatial and temporal distribution of cases indicated that the epidemic spread from the Seronera area throughout the ecosystem at a rate of 10–20 km/month (Fig. 2). By the end of 1994 the epidemic had reached the lions of the MMNR in the north and domestic dogs of the NCA in the south. Because cases in NCA dogs followed those in lions, we inferred that the pastoralist (Masai) dog population was unlikely to be either the reservoir or source of CDV for wildlife in the Serengeti in 1994.

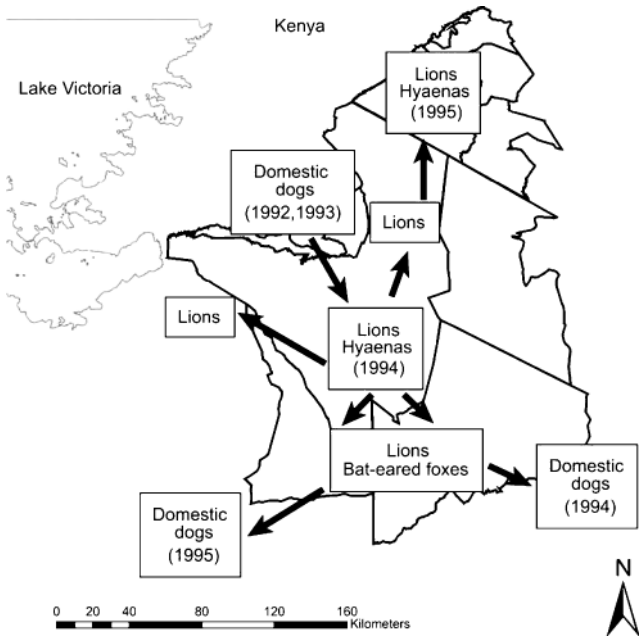

Figure 2. Location and timing of canine distemper cases in the Serengeti, with the likely direction in which the epidemic spread from its likely source in high-density domestic dog populations to the northwest of the Serengeti National Park.

CDV Serological Studies

As a result of practical difficulties in sample availability and field diagnostics, epidemiological studies in wildlife draw heavily on serological data. Nevertheless, serology has limitations and, for most diseases (including CDV), seropositivity demonstrates only that an animal has been exposed to a pathogen at some time in the past. To ascertain the precise timing of exposure and to distinguish epidemic and endemic patterns, longer-term data are needed together with information on the age of individuals. The Serengeti lion project is a rare example of a long-term large-mammal study that combines both sets of data. As such, it has been possible to obtain precise information on the timing of CDV exposure in the lion population, with a consistent stepwise pattern across the years providing evidence for exposure to CDV in 1981 and 1994 but not in the intervening years (Packer et al. 1999; Fig. 3). If CDV had been maintained in a wild carnivore reservoir over

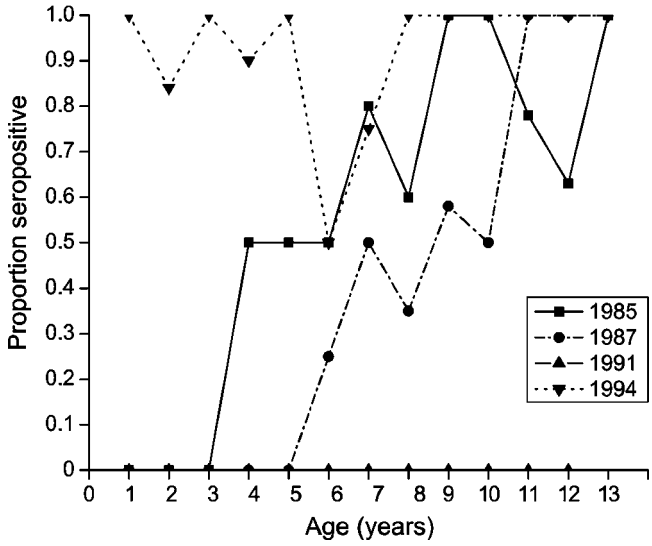

Figure 3. Canine distemper virus age-seroprevalence patterns in the Serengeti lion study population sampled in 1985, 1987, 1991, and 1994.

this period, we would have expected occasional seropositive individuals to have been detected throughout the period between 1981 and 1994 without such a strong age-related structure of seropositivity. Similarly, data collected on MMNR hyaenas between 1992 and 2001 showed that juveniles were exposed to CDV only in 1994 and 1995 and again in 2000 and 2001 (Harrison et al. 2004), suggesting a lack of virus persistence in the population. We therefore conclude that wildlife populations were unlikely to have been the reservoir for CDV before the 1994 epidemic.

Short-term serological data are much less informative than long-term serological profiles. A single cross-sectional survey of the lions in 1985 (Fig. 3) would have been misleading because a rising age-prevalence pattern could also have been explained by continuous circulation of CDV in the lion population and a higher cumulative exposure in older animals. In this case it would have been impossible to exclude wildlife as reservoirs and an inappropriate disease control strategy might have been recommended.

Similar conclusions can be drawn from CDV age-seroprevalence data in domestic dog populations. Age-seroprevalence data collected over several years (Fig. 4a-b) have provided two important pieces of information: (1) evidence of exposure to CDV in 1991, consistent with observations of clinical signs of CDV in domestic dogs in Loliondo in 1991 (Cleaveland 1996) and coincident with the time when African wild dogs disappeared from the Serengeti and (2) evidence that, in the 2 years prior to the 1994 epidemic, CDV was present in the high-density dog population of Serengeti District; but with zero seroprevalence in young dogs in Ngorongoro District, CDV was not likely to have been circulating in this low-density

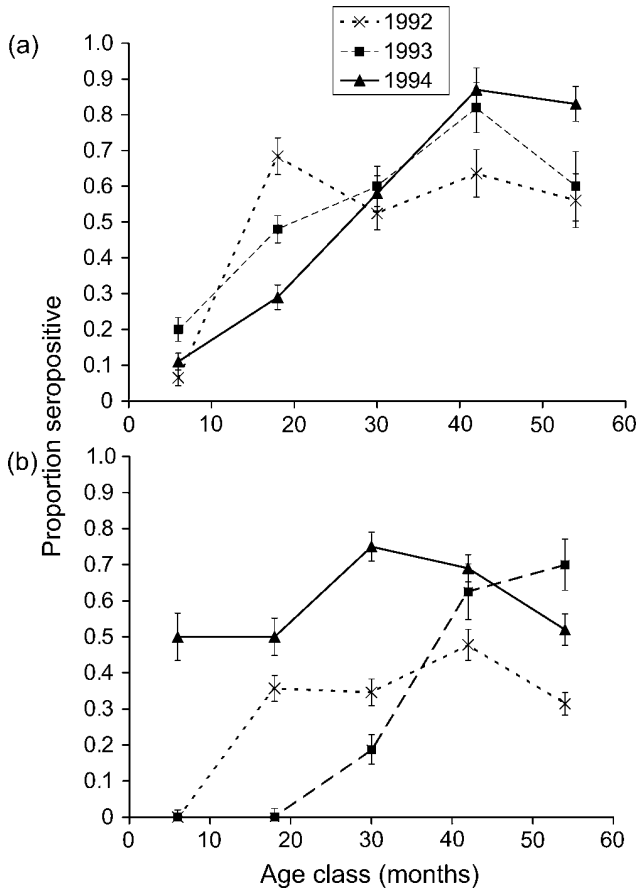

Figure 4. Canine distemper virus age-seroprevalence patterns in various age classes of domestic dogs sampled between 1992 and 1994 in (a) Serengeti District and (b) Ngorongoro District.

population in 1992 or 1993. These longitudinal data, in combination with wildlife age-seroprevalence data thus provide evidence that higher-density dog populations to the west of the Serengeti were the likely source of CDV in the 1994 epidemic (Cleaveland et al. 2000).

CDV as a Threat to Wildlife

The intensive monitoring of individually recognized lions over the past 40 years has elucidated the relative importance of infectious diseases in long-term population dynamics. Although CDV caused an unprecedented decline in the Serengeti lion population in 1994, lion numbers recovered rapidly to pre-epidemic levels as a result of high cub survival (Fig. 5). In contrast, in the nearby Ngorongoro Crater, a CDV outbreak, which occurred in combination with tick-borne diseases in 2001, caused 35% mortality in the small Ngorongoro lion population and has prevented recovery to its carrying capacity (Kissui & Packer 2004).

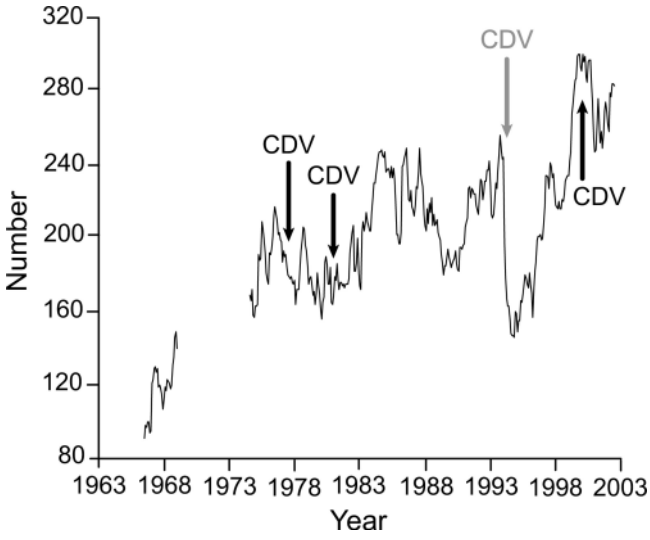

Figure 5. Size of the Serengeti lion population and two kinds of events of canine distemper virus (CDV) over time (gray arrow, 1994 epidemic that caused high mortality in the population; black arrows, periods when lions were exposed to CDV with no apparent disease outbreak).

A further difficulty in evaluating the CDV disease threat, particularly in comparison with rabies, is the apparent variability in CDV pathogenicity in Serengeti lions. Although disease incidence and mortality were both high in lions during the 1994 epidemic, no disease signs or disease-associated mortality were recorded during the 1981 outbreak. Similarly, serological data collected between 1995 and 2004 have indicated exposure of lions to CDV since 1994 but with no associated morbidity or mortality (S.C., C.P. & T.L., unpublished data; Fig. 5). In Ngorongoro the population has been exposed to CDV on at least two occasions; one was associated with high mortality (in 2001) and the other caused no apparent illness (in 1980; Packer et al. 1999; Kissui & Packer 2004).

Many questions exist about the determinants of CDV pathogenicity in lions, and hypotheses are now being generated to explore links between CDV pathogenicity, virus strain, host factors (e.g., nutritional status), and other cofactors (e.g., climate, intercurrent tick-borne diseases; Kissui & Packer 2004). The value of long-term data is in no doubt; with data from the Serengeti in 1981 only, one might conclude that CDV is a totally benign pathogen of lions, whereas with data from 1994 alone one might conclude that CDV is invariably highly pathogenic. The true complexity of the situation is only now becoming apparent with data spanning multiple outbreaks over many years.

Domestic Dogs as Part of the Serengeti Mara Ecosystem

Preliminary epidemiological studies highlight several additional aspects of the ecology of domestic dogs that are relevant to the conservation management of the SME. In 1994 approximately 30,000 dogs lived within 20 km of the park boundaries. Populations were growing at a rapid rate (5–10% per annum), and there was frequent contact between domestic dogs and wild carnivores (Cleaveland 1996). It became clear that domestic dogs comprised an important component of the SME, which had previously not been considered in conservation management. Disease transmission from expanding domestic dog populations may increasingly constitute an anthropogenic edge effect around protected areas (Woodroffe & Ginsberg 1998) and poses a particular threat to wide-ranging species, such as wild dogs. Awareness generated by research in the Serengeti has contributed to the development of several new studies of the epidemiology of domestic dog diseases in and around protected areas in Africa (e.g., Laurenson et al. 1997; Butler et al. 2004) and South America (Fiorello et al. 2004; Schenck & Stail 2004). Similar concerns about the transmission of disease from humans to populations of wild apes have also resulted in the establishment of the great ape health monitoring unit as a priority for conservation of great apes (see http://pin.primate.wisc.edu/idp/idp/entry/601).

Intervention Trials Involving Mass Dog Vaccination

Intervention trials, involving mass vaccination of domestic dogs against rabies and CDV, were implemented to provide more definitive evidence about the role of dogs as reservoirs for rabies and CDV in the Serengeti. This approach had the additional advantage of reducing the incidence and burden of disease in human and domestic animal populations of local communities.

With CDV and rabies persisting only in higher-density dog populations, the populations bordering the western boundaries of the Serengeti (Fig. 1) were considered the major disease threat and the focus of the first intervention trials, initiated in Serengeti District in 1996. These trials, which adopted a simple central-point vaccination strategy, resulted in a vaccination coverage of 60–70% of domestic dogs, which was sufficient to bring rabies under control in domestic dogs (Cleaveland et al. 2003) and demonstrated the possibility of reducing anthropogenic impacts of dog diseases in the Serengeti. Nevertheless, rabies continued to persist in other districts, and since 2003, vaccination campaigns have been extended to all districts adjacent to the park in an attempt to "ring vaccinate" the Serengeti and minimize transmission of dog rabies to wild carnivores within the park.

The need to monitor disease in wildlife and domestic animal populations as part of the intervention trial provided a catalyst for the development of disease surveillance networks within and adjacent to the park, resulting in greater integration between research and park management and in improved collaboration between wildlife and livestock veterinary officers. Carnivore disease monitoring is now a core element of Tanzania National Parks (TANAPA) activities, and rabies vaccination in domestic dogs has been carried out by TANAPA after dog rabies outbreaks adjacent to other parks, including Arusha, Ruaha, and Udzungwa (TANAPA 2001, 2002). Sustainability of these programs remains a challenge, but increasing involvement of district councils and TANAPA in the implementation of dog vaccination campaigns provides grounds for optimism. In the longer term a national rabies control strategy for Tanzania is under development, which integrates the wildlife sector with public health agencies and veterinary services as a means of securing intersectoral collaboration and funding.

Recognition of the need for epidemic surveillance in wildlife has led to the initiation of a small carnivore monitoring program (in which distance-sampling techniques are used), which has now become a routine part of SNP management activities involving both park ecologists and research scientists. Finally, the importance of disease as a threat to endangered species and to conservation targets has clearly been recognized by wildlife authorities and planning for disease management is now integrated into the new SNP General Management Plan (TANAPA 2005).

Integrating Public Health and Conservation Initiatives

In addition to influencing park management activities, the intervention trials have also had implications for conservation through impacts on public health. As a result of mass dog vaccination, demand for costly human rabies vaccine for postexposure rabies prophylaxis has declined significantly (Cleaveland et al. 2003), providing economic benefits that may help sustain any future control programs. Furthermore, dog vaccination programs have contributed to improved relations between the park authorities and local communities. More broadly, this approach is likely to be an area of growing interest, given the fact that many emerging human diseases have links with wildlife (Cleaveland et al. 2001; Cleaveland 2003). Because few tools are available to control infections of wildlife, measures to control diseases associated with wildlife reservoirs have often resulted in harm to wildlife (e.g., culling of bushbuck to control sleeping sickness in East Africa and culling of badgers to control bovine tuberculosis in the United Kingdom). Disease control strategies that integrate wildlife expertise will not only ensure more conservation-friendly approaches to public health problems but will also broaden the scope of funding opportunities to support conservation-related activities.

Relevance of Disease Modeling for Conservation

The principle role that models have played in the shaping of conservation management and policy is through the application of population viability analyses (PVAs; Beissinger 2002). Disease has long been recognized as a significant source of mortality in PVAs, but it is only relatively recently that the models that underlie these analyses have included an explicit representation of infection dynamics (Lafferty & Gerber 2002; Haydon et al. 2002*b*), rather than simply imposing a fixed characteristic pattern of mortality on the host species. Explicit representation of these dynamics is essential if models are to indicate the sensitivity of results to uncertainties in the underlying epidemiological parameters (Harwood 2000) and to evaluate the impacts of different control strategies (Haydon et al. 2002*b*). An epidemiological model, suitably integrated into a population viability analysis can be used to address many management-related questions. For example, what is the extinction threat posed to a population from a disease left uncontrolled? What is the relative reduction in risk of extinction from vaccinating different proportions of the host population? Given a fixed vaccination effort, how is it best distributed among the population? As with any PVA it is unwise to attempt to quantify absolute measures of risk or impact, but such models do allow a quick, cheap, and easy way of comparing the effects of different strategies and identifying processes about which important uncertainty remains.

Construction, parameterization, and integration of epidemiological models into population viability models benefit enormously from long-term multidisciplinary studies (Creel & Creel 2002; Haydon et al. 2002*b*). Host demographic parameters (birth and death rates, age, and/or social structure) are fundamental to many epidemiological models as are pathogen-related demographic parameters (incubation and infectious periods, morbidity, seropositivity, and duration of immunity), and these can often only be reliably determined from long-term studies of host ecology and pathogen epidemiology. Long-term epidemiological studies are also essential to determine whether the model should focus on endemic or epidemic pathogen dynamics and to direct the reservoir structure assumed by the model.

Once a plausible model has been constructed that provides a representation of the status quo, different control scenarios can be modeled and their effectiveness compared. Much epidemiological control theory relates to the elimination of pathogens, or at least the avoidance of substantial disease outbreaks. Although this is a laudable goal, it is one that arises largely from a human disease control perspective (Anderson & May 1991). The objective of

disease control within a conservation framework may be directed at ensuring population viability rather than disease elimination—and this distinction can be important, particularly when considering small wildlife populations, surrounded by large reservoirs of infection. For example, results of modeling studies of rabies in African wild dogs suggest that core vaccination campaigns that target <40% of individuals within a population would ensure persistence of small populations by preventing the largest outbreaks that reduce the population below a minimum viable population size (Vial et al 2006). The distinction between ensuring disease elimination and population viability could be critical for a resource-limited conservation program; the first will often be a bridge too far, the second a realistic and attainable goal.

Conclusions

Outbreaks of rabies and CDV in the Serengeti and the research initiated in response to these outbreaks have had important implications for conservation management and policy in Tanzania and further afield. The Serengeti outbreaks demonstrated that CDV and rabies were pathogens that had the potential to cause major population declines (in the case of CDV and lions) and to pose an immediate extinction threat (in the case of rabies and African wild dogs). A key contribution of these research studies has been to demonstrate the role of domestic dogs in the Serengeti as a source of CDV in the 1994 epidemic and as a potential reservoir of both rabies and CDV. These findings all have considerable conservation application in terms of designing disease control programs to reduce the anthropogenic threat of introduced canid diseases and to minimize extinction threats to wild carnivores. One of the major practical applications of the research relates to the design of effective and appropriate disease control measures, with experience gained from wild dog vaccination programs highlighting the importance of robust study design and mass vaccination trials in domestic dogs demonstrating the feasibility and cost-effectiveness of dog vaccination. Perhaps the major contributions, however, have been an enhanced awareness of domestic dog diseases as a threat to wild carnivores, a greater understanding of the need for disease monitoring and investigation within national parks, the recognition of the benefits of collaboration between different research disciplines, and the importance of integrating research and management within wildlife authorities, veterinary authorities, and public health sectors.

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